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ON THE CLASSIFICATION OF THE TESTUDINATA.

BY GEORGE BAUR.

BOULENGER, Döderlein, Zittel, and Lydekker have lately published more or less extensive works on the Testudinata. All these publications I have to discuss first before I shall undertake to give my own views on the natural arrangement of the group.

I begin with Boulenger. A general classification of the Testudinata was given by him in 1888 in the 23d volume of the 9th edition of the *Encyclopædia Britannica*, pp. 456-457.

The whole group was, after Dollo, divided into two sub-orders, I. *Athecæ*, II. *Testudinata*.

The *Athecæ* contained the single family "*Sphargidæ*," with the genera *Dermochelys*, *Psephophorus*, *Protosphargis*, *Protostega*, *Psephoderma*?; the *Testudinata* all the other Tortoises, which were divided in *Cryptodira*, *Pleurodira*, and *Trionychoidea*.

In the year following this classification was adopted by Boulenger in his catalogue of Chelonians¹, but the name of the second sub-order was changed into *Thecophora*. The whole order was called *Chelonia*.

A few months later Döderlein² published a classification of Testudinata. He distinguishes four sub-orders: *Atheca*, *Trionychoidea*, *Cryptodira*, *Pleurodira*.

Nearly at the same time the first part of the *Reptilia* of Prof. Zittel's "*Handbuch der Palæontologie*"³ appeared, containing the Testudinata.

Zittel accepted three sub-orders of the Testudinate; *Trionychia*, *Cryptodira*, *Pleurodira*. The *Athecæ* are not accepted, but considered a family of the *Cryptodira*.

¹ Boulenger, George Albert. Catalogue of the Chelonians, Rhynchocephalians and Crocodiles in the British Museum (Natural History), London, 1889, pp. 4-6.

² Elemente der Palæontologie, pp. 633-634.

³ Zittel Karl G. Handbuch der Palæontologie. Vol. III., part 3. München und Leipzig, 1889, pp. 513-547.

Lydekker calls the whole order Chelonia, which he divides into two sub-orders, *Athecata* and *Testudinata*.

The Athecata correspond to the Athecæ; the Testudinata contain four sections: 1. *Amphichelydia*; 2. *Pleurodira*; 3. *Cryptodira*; 4. *Trionychoidea*. In the *Amphichelydia* are placed the Pleurosternidæ. "This section is formed for the reception of certain extinct Chelonians, mostly of Mesozoic age, which combine in a remarkable manner the characters of the two following sections [*Cryptodira* and *Pleurodira*], and may probably be regarded as the survivors of the earlier ancestral types from which those two sections took origin."

THE ORDINAL NAME FOR THE TORTOISES.

Boulenger and Lydekker use the name Chelonia; Zittel and Döderlein the name Testudinata. The name Chelonia has no right to stand, and must give place to that of *Testudinata*, as will be seen from the following table:

Boulenger, p. 4.—Order, *Chelonia*.

Cheloniens, Brongniart, Brit. Soc. Philos., II., 1800.

Testudinata, Oppel, Order Rep., 1811.

Baur.—*Testudinata*, Klein, 1751.

1751. *Testudinata*, Klein, Jac. Theod., Quadrupedum Dispositio brevisque Hist. Nat., 1751, p. 96.

1799. *Cheloniens*, Brongn, Mag. Encycl. ou Journ. des Sciences, des Lettres et des Arts, par A. L. Millin, T. VI., An. VII., 1799, pp. 184-201.

1802. *Testudines*, Treviranus, G. R., Biologie, Bd. I., p. 260, Göttingen, 1802.

1806. *Testudines*, Shaw, G., General Zool., Vol. III., Part 1., p. 5., London, 1802.

1806. *Chelonii*, Dumeril, A. M. C., Zool. Anal., Paris, 1806, p. 76.

⁴ Lydekker R., in Henry Alleyne Nicholson and Richard Lydekker. A Manual of Palæontology, Vol. II., part III. Edinburgh and London, 1889, pp. 1082-1118. And Lydekker, Richard, Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History), Part III., containing the order Chelonia. London, 1889.

1822. *Chelonea*, Fleming, Philos. of Zool., Vol. II., p. 268, Edinburgh, 1822.

1825. *Fornicata*, Haworth, A. Tilloch, Phil. Mag., LXV., 1825, pp. 372-373.

1828. *Sterrichrotes*, Ritzen, F. F. A., Nova Acta Nat. Cur., 1828, Vol. XIV., Bonn, 1828.

1834. *Chelonia*, Carus, G., Lehrbuch der Vogl., Zool. Aufl. I., Theilp. 25, Leipzig, 1834.

The Athecæ.—I have shown in a paper published some time ago,⁵ that the group Athecæ, or Athecata, as spelled by Lydekker, is an unnatural one, and that its members belong to the Pinnata, or sea-tortoises. I do not need to discuss this question fully again on this plate; I shall only give my principal reasons.

Protostega and Protosphargis, which are placed by Boulenger, Lydekker, Döderlein, among the Athecæ, are near the Cheloniidæ. In both true marginal bones (peripheralia) are developed. The skull of Protostega is like that of the Cheloniidæ; there is a free epipterygoid, and the descending processes of the parietals are present; also an ossified articular bone. Humerus and coracoid are in shape between those elements in Dermochelys and Cheloniidæ. It seems that Lydekker is inclined lately to accept my idea of the relationship of the Athecæ, for he says in the introduction to his Catalogue of Fossil Tortoises: "If the skull referred by this writer (Baur) to Protostega be rightly assigned, there will be evidence of a closer connection between the two groups (Cheloniidæ and Protostegidæ) than has hitherto been supposed. The skull from which I took these remarks is certainly rightly assigned," for it is the type of Protostega, and all the above points are mentioned by Prof. Cope⁶ in his description, with figures, of Protostega; even Lydekker, who still sustains the Athecæ, will have to admit now that at least the Protostegidæ

⁵ Baur, G. Die systematische Bemerkungen über die systematische Stellung von Dermochelys, Blainv. *Biol. Centralbl.*, Vol. IX., Nos. 5, 6. 1889, pp. 149-153; 180.191.

Nachträgliche Bemerkungen über die esystematische stellung von Dermochelys Blainv., *Biol. Centralbl.* Vol. IX., Nos. 20, 21, pp. 617-619; see also my notes in *Zööl. Anz.*, No. 238, 1888, 1886; *Science*, Vol. XI., No. 268, 1888; *Zööl. Anz.*, No. 285, 1888, and No. 298, 1889.

⁶ Cope, E. D., The Vertebrata of the Cretaceous Formations of the West. Rept. U. S. Survey Territ., Vol. II., 1875.

are very near the Cheloniidæ, and belong certainly to the Pinnata. After it shall have been proved that in Protostega and Protosphargis an entoplastron is always absent, they will rank as a distinct family from the Cheloniidæ, to be placed between the latter and the Dermochelyidæ. I have shown now that Protostega and Protosphargis are true Pinnata; we have now to consider the remaining genera of the group: Dermochelys, Psephophorus, Eosphargis, and Psephoderma. I do not consider Psephoderma at all in this connection; it is, so far, impossible to determine the exact systematic position of this genus. Such dermal ossification as seen in Psephoderma may appear in any order of the Reptilia. I have shown that the absence of the descending processes of the parietals in the remaining three genera is an entirely secondary condition, that all Testudinata possessed originally an epipterygoid and the descending processes, and that in the Pinnata the tendency is present to abort these processes. I have shown that the character given by Boulenger to Dermochelys, that the lower border of the postfrontal joins the jugal and the squamosal, and is separated from the quadratojugal by the two latter bones, does not hold, for it is also found in specimens of Chelonia. But to convince everybody that Dermochelys and its fossil allies, Psephophorus and Eosphargis, cannot be separated from the Pinnata, I give the characters which are only found in the Pinnata, and in no other group of the Testudinata. These characters are:

1. The foramen palatinum, between palate and maxillary, is absent.
2. The articular faces between the sixth and seventh cervicals are plane.
3. The nuchol has a distinct process on the lower side for the articulation of the neuroid of the eighth cervical.
4. The small trochanters of the femur are united, and there is a fossa between these and the large trochanters. (This condition is also seen in the true land tortoises, Testudinidæ).
5. There is only one central line in the carpus; the intermedium reaches the first carpale, excluding the centrale from the radiale.

The characters, with the exception of No. 4, are typical for the Pinnata, but they are also typical for Dermochelys. *That the Dermo-*

chelyidæ represent a specialized branch of the Pinnata there cannot be any doubt whatever. The mosaik-like carapace and plastron of these forms is probably a secondary formation, which appeared after the dermal part of the ribs had disappeared entirely. The oldest Dermochelyidæ known are from the lower Eocene (Eosphargis). True Cheloniidæ are known already from the Cretaceous, and the intermediate Protostegidæ are from the same formation; it is probable that the *Protostegidæ* have to be considered as the ancestor of the *Dermochelyidæ*.

After it has been shown that the Athecæ are an unnatural group, and belong to the Pinnata, we have to consider the other divisions proposed. Boulenger, Lydekker, Döderlein, Zittel, all accept the groups Pleurodira, Cryptodira and Trionychia; these groups are certainly natural, as will be admitted by everybody; a new section was introduced by Lydekker under the name of Amphichelydia (*Quart. Jour. Geol. Soc.*, XLV., p. 518, 1889). "They are characterized by having a shell constructed on the plan of that of the Cryptodira and Pleurodira, in which mesoplastral bones and an intergular shield are developed. The pubis may articulate, without sutural union, with the xiphiplastral."

The skull and neck are unknown. The coracoid and humerus (when known) are of a Pleurodiran type (Lydekker, Cat., pp. 204, 205). This group is also natural, and corresponds to a sub-order to which I have given a different name in MSS., and the characters of which I can point out in full. The material on which these characters are based consists of nearly all parts of the skeleton, including skull and cervicals of *Compsemys plicatulus* Cope, the oldest American Tortoise, from the Jurassic of the Rocky Mountains. Most of the material was examined at the Peabody Museum, New Haven, Conn. Especially I have to state the interesting fact that *Compsemys* has a complete mesoplastron, and resembles very much Pleurosternum. This is another support for the view that the Camarasaurus beds correspond to the Purbeck and Oolite of England.

I give now the characters of the five sub-orders of Testudinata, which I adopt:

I. *Amphichelydia*.

Nasals free; a squamoso-parietal arch; descending processes of prefrontals joining vomer; stapes in an open groove of the quadrate; pterygoids narrow in the middle, without wing-like lateral expansions, separating quadrate and basisphenoid; epipterygoid well developed and free; dentary bones distinct. Cervical vertebræ with well-developed transverse processes, more in front of vertebra, with single articular faces, biconcave; dorsal vertebræ, sacral vertebræ, with well-developed ribs; ribs of sacral vertebræ connected with centrum and neuroid. Pelvis not anchylosed to the carapace and plastron. Epiplastra in contact with hyoplastra, entoplastron oval or rhomboidal; a complete series of peripheralia connected with the ribs.

II. *Pleurodira*.

Nasals free, or united with prefrontals; a squamoso-parietal arch present or absent; descending processes of prefrontals absent; stapes in a groove of quadrate generally closed on the outside; pterygoids broad, forming wing-like lateral expansions, not separating quadrate and basisphenoid; epipterygoid not free; dentary bones distinct and united. Cervical vertebræ with well-developed transverse processes generally in middle of vertebra, with single articular faces; sacral ribs rudimentary; sacral ribs connected with neuroids. Pelvis anchylosed to carapace and plastron. Epiplastra in contact with hyoplastra, entoplastron oval or rhomboidal; a complete series of peripheralia connected with the ribs.

III. *Cryptodira*.

No free nasals; a parieto-squamosal arch present or absent; descending process of prefrontals connected with vomer; stapes in an open grove, entirely covered by the quadrate behind; pterygoid narrow in the middle, without wing-like lateral expansions, separating quadrate and basisphenoid; epipterygoid free, or not free; dentary bones united. Cervical vertebræ with rudimentary transverse processes in front of vertebra; the posterior

cervicals with double articular faces; sacral ribs well developed, and connected with centrum and neuroids. Pelvis free from plastron and carapace. Epiplastra in contact with hyoplastra, entoplastron oval, rhomboidal or T-shaped; a more or less complete series of peripheralia more or less connected with the ribs.

IV. *Chilotæ* (Trionychia).

No free nasals; no parieto-squamosal arch; descending processes of prefrontals connected with vomer or not; stapes entirely surrounded by quadrate; pterygoids broad, without wing-like lateral expansions, separating quadrate and basisphenoid; epipterygoid free; dentary bones united. Cervical vertebræ with very rudimentary transverse processes in front of vertebra; the posterior cervicals with double articular faces; sacral ribs well developed, and connected with neuroids only. Pelvis free from plastron and carapace; epiplastra separated from hyoplastra by the V-shaped entoplastron; marginal bones absent, or forming an incomplete series, not connected with the ribs.